



Some perspectives on the biology and ecology of nudibranch molluscs: generalisations and variations on the theme that prove the rule

Christopher D. Todd¹, Walter J. Lambert^{1,2} and Jon Davies^{1,3}

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ABSTRACT Aspects of the ecology and reproduction of nudibranch molluscs are addressed in terms of the generalisations often applied to the group. We summarise the present applications of nudibranchs as model systems and highlight their potential for investigating other ecological problems. A commonly held view is that species of the Order are characterised by being specialist predators. The available literature supports this generalisation: approximately 50% of the species of known diet are associated with just one prey species (monophagous) and many stenophagous species probably prefer just one or two species. Even those generalists that prey upon a number of species still are specialised at higher taxonomic levels, in being obligately associated with, for example, only sponges, bryozoans or anemones. With respect to life cycles and life history, we present data for the dorid *Cadlina laevis* which show this species to be unique in the literature in displaying a perennial life cycle, spawning just once per year, and surviving to perhaps 5 or 6 years of age. This is in marked contrast to the typical annual/subannual life cycles and semelparous life history reported for other species. Given the difficulties in undertaking field population studies, we question how representative are the reported species, which form the basis of generalisations for the Order. Intraspecific variation in egg sizes is discussed in terms of empirical data for several intertidal populations of the dorid, *Adalaria proxima*, striking within and between population variation in egg sizes indicates marked differences in larval 'quality', but whether these differences are adaptive, or nonadaptive consequences of genetic drift of closed populations, remains open to further study. The potential evolutionary importance of egg size variation in relation to shifts in mode of larval nutrition from planktotrophy to lecithotrophy also is discussed. The generalisation that this Order also is characterised by simultaneous hermaphroditism is valid, but not without exception. Laboratory studies have shown that *Pbestilla sibogae* is functionally male at an extremely small size and that sperm received and stored at otherwise juvenile body sizes are disproportionately successful in fertilising an individual's oocytes; in terms of sperm competition models this is a clear example of first male/partner precedence. Finally, the phenomenon of poecilogony — switching of larval strategies within species populations — is discussed in the light of recent examples amongst nudibranchs and ascoglossans. If a real and widespread (albeit rare) phenomenon, the fuller understanding of poecilogony presents larval ecologists with a considerable challenge.

RIASSUNTO Alcuni aspetti dell'ecologia e delle strategie riproduttive nei molluschi nudibranchi e i modelli funzionali che ne derivano hanno una grande importanza anche per la comprensione di problematiche ecologiche d'interesse generale. I nudibranchi sono generalmente considerati predatori specialisti: circa il 50 % delle specie studiate è monofago e gli stenofagi predano, di norma, due-tre specie. Le specie generaliste sono inoltre strettamente legate a ben determinati livelli tassonomici siano questi poriferi, briozoi o cnidari. Il ciclo vitale del doridaceo *Cadlina laevis* sembra essere particolare, presentando una riproduzione all'anno e concludendosi in forse 5-6 anni. Ciò è in contrasto con i tipici cicli annuali o subannuali e la semelparità delle altre specie di nudibranchi. Considerando la difficoltà di condurre ricerche di campo in questo settore questi risultati suggeriscono una certa cautela nel generalizzare i cicli vitali in questo Ordine. Variazioni intraspecifiche nel diametro delle uova in diverse popolazioni del doridaceo intertidale *Adalaria proxima* inducono a pensare che possano esserci differenze significative nella "qualità larvale" in popolazioni diverse; se tali differenze siano adattative o meno, cioè conseguenza di un drift genetico di popolazioni isolate, rimane un problema insoluto. Viene anche discussa l'importanza evolutiva delle variazioni nelle dimensioni delle uova in funzione d'eventuali passaggi da una strategia planctotrofica ad una lecitotrofica. I nudibranchi presentano, generalmente, un ermafroditismo simultaneo, ma non mancano le eccezioni. Studi di laboratorio hanno dimostrato che individui di taglia molto piccola di *Pbestilla sibogae* sono maschi funzionali, ma gli allospermi acquisiti a qualsiasi taglia giovanile hanno modeste probabilità di fecondare gli oociti dell'individuo: questo modello di "sperm competition" è un chiaro "first male/partner precedence". Infine, il fenomeno della pecilogonia — l'eliminazione della fase larvale all'interno di singole popolazioni — viene discusso alla luce di recenti esempi tra nudibranchi e ascoglossi. Se questo processo sia reale, diffuso o, al contrario raro, rimane un importante spunto di ricerca per l'ecologia larvale.

C. D. TODD¹, W. J. LAMBERT^{1,2} AND J. DAVIES^{1,3}

¹ Gatty Marine Laboratory, Division of Environmental & Evolutionary Biology, School of Biology University of St Andrews, St Andrews, Fife, Scotland. KY16 8LB - cdt@st-andrews.ac.uk

² Present address, Department of Biology, St. Anselm College, Manchester, New Hampshire 03102 USA - wlambert@cisunix.unh.edu

³ Present address, JNCC, Monkstone House, City Road, Peterborough, PE1 1JY - davies_j@jncc.gov.uk

INTRODUCTION

Experimental biologists have constantly sought species to provide model systems for specific topics of research. Of these, a limited number do become utilised worldwide in certain fields; *Drosophila* and *Caenorhabditis elegans* Maupas are perhaps pre-eminent examples in genetics and developmental biology. The advantage of one or a few species providing a model for a wide array of research is the knowledge base upon which any new approaches can be built. But one of the consequences is that it

perhaps becomes easy to lose sight of the variation that is the very essence of biology. Ecophysiological research on the widely distributed blue mussel, *Mytilus edulis* L., has proven this to be a most valuable model organism both for empirical and modelling studies concerning marine pollution; from this there have developed numerous monitoring programmes successfully deploying molluscs as sentinel organisms in pollution studies (e.g. Mussel Watch programmes, BELIAEFF *et al.*, 1998; CANTILLO, 1998; LAUENSTEIN & DASKALAKIS, 1998). However the benefits of



comparability of responses for a single species at different localities must be weighed against the possible costs of lack of representativeness.

Particular species of nudibranchs have proven to be excellent model species for many aspects of physiological, cell biological and ecological research. Most of these topics are out-with the bounds of the present paper, but particularly prominent examples include:

1. Fundamental neurobiology, and especially neural control mechanisms and central pattern generators; e.g. the escape swimming response of *Tritonia diomedea* Bergh (e.g. WILLOWS *et al.*, 1973; KATZ, 1998),

2. Behaviour and physiology; e.g. the neural basis of associative learning in *Hermisenda crassicornis* (Eschscholtz) (e.g. ALKON, 1984; BLACKWELL & ALKON, 1999),

3. Developmental biology; e.g. the induction and control of larval metamorphosis and morphogenesis in *Phestilla sibogae* Bergh (e.g. HADFIELD, 1977, 1998; HADFIELD & PENNINGTON, 1990).

One objective here is to highlight the further potential that the Order Nudibranchia possibly provides to ecologists as model organisms or systems. Another is to discuss certain aspects of ecological variability, the study of which might prove to be especially tractable with nudibranchs. Third, it is perhaps timely also to reassess the validity of some of the generalised perceptions that are invariably ascribed to this fascinating and varied group of molluscs. When deriving generalisations about the ecology of natural groupings of diverse species, such as the nudibranch molluscs, periodic appraisal should be made of how representative are the studied species, and hence the information base. The degree of dietary specialisation displayed by the four suborders is specifically discussed and the typical life cycles and life history which are held to characterise the order are examined in the light of new data on *Cadlina laevis* (L.).

There are pitfalls in presuming that a single model system explains similar patterns or processes in other species or biotopes. An illustrative example concerning nudibranchs is the remarkable phenomenon of spine elongation as an inducible, adaptive, morphological plasticity amongst bryozoans. HARVELL (1986, 1991, 1998) has undertaken detailed and elegant investigations of the environmental induction of elongate spine formation in colonies of the cheilostomatid bryozoan *Membranipora membranacea* (L.). Elongate spine induction is a phenotypically plastic response by zooids within a colony in mounting a defence against *Paradoridella* (= *Doridella*) *steinbergae* (Lance), a specialist nudibranch predator. Induction of spines is rapid (1-2 d) and the response can be elicited by contact with the predator or by waterborne exudates therefrom. Other studies of inducible morphologies for a wide array of invertebrate taxa also reveal the inductive agent to be biological in origin, and commonly attributable to predator species (ADLER & HARVELL, 1990); given that nudibranchs worldwide are major predators of bryozoans it might be expected that other cases of elongate spine induction in bryozoans also will be attributable to predation.

In NW European waters *Electra pilosa* (L.), which also is a member of the family Membraniporidae, is preyed upon by numerous species of nudibranchs and is the preferred diet of several specialists, including the dorid *Adalaria proxima* (Alder & Hancock). Like *M. membranacea*, *E. pilosa* also displays morphs in certain localities with grossly elongated (proximal) spines. From Harvell's work on *M. membranacea* we considered that spine induction in *E. pilosa* possibly was a response to these specialist predators, and perhaps specifically to *A. proxima*. Although predation of *E. pilosa* zooids by *A. proxima* is reduced for long-spined colonies, early field observations did not support this conjecture. Laboratory experiments subsequently confirmed that elongate proximal spines are not induced by *A. proxima*, or other potential predators, but that this plasticity is unique in being induced by an abiotic factor. Induction is only by wave crash-related abrasion of the bryozoan by other macroalgae (BAYER *et al.*, 1997) and wave crash alone would not induce the formation of elongate spines. The partial protection from nudibranch predation afforded to *E. pilosa* colonies by elongate spines is thus fortuitous and this system evidently is quite different to that seen in *M. membranacea*.

The present coverage of topics is deliberately eclectic and not intended to be comprehensive; this is very much a biased perspective of problems of interest regarding particular aspects of their ecology, especially their reproduction, but also we are acutely conscious that these generalisations may not be general at all, but merely reflect personal perceptions or ignorance. Our perspective also is decidedly boreo-centric in that our direct experience of these molluscs in tropical and polar waters is limited and even at temperate latitudes our studies have focused on North Atlantic species and systems.

GENERALIZATIONS PERTAINING TO NUDIBRANCH MOLLUSCS

Despite the considerable morphological and ecological diversity of the Order Nudibranchia, there are embedded in the literature a number of general perceptions about the ecology and biology of the group which perhaps require re-evaluation; if there are marked exceptions to these rules, or if the contentions are not supported by the available empirical data, it is clear that we might be constrained in our perspective. Through our own interests in nudibranchs, we can identify three generalizations or particular features of their biology in this context: these species typically are held to (i) display stenophagous (specialist) prey associations, (ii) to undergo annual/subannual life cycles and to have strictly semelparous life histories, and (iii) to be simultaneous hermaphrodites. Given that nudibranchs are distributed at all latitudes throughout the World Ocean, and occur at all depths from the intertidal to the deep ocean benthos — even at extreme environments such as hydrothermal vents (VALDES & BOUCHET, 1998) — such generalisations obviously require qualification and there are certain to be exceptions. The question is are there sufficient exceptions to warrant reappraisal of the rules?



STENOPHAGOUS PREY ASSOCIATIONS

The term "specialisation", as a categorisation of a species' dietary association(s), is a value judgement and open to various interpretations. As a basis for illustrating ecological trends throughout the Nudibranchia, we here have subjectively categorized all monophagous (single prey species) and stenophagous (2 or 3 prey species) nudibranchs as being "specialists". McDONALD & NYBAKKEN (1997) undertook the considerable task of appraising all the primary sources published prior to 1996 on the recorded diets of nudibranchs throughout the World Ocean. From their database the diets of 600 species representing all four suborders have been extracted. A few species were deleted because of the lack of taxonomic rigour or sufficient detail in the reported dietary species; for example, the only dietary information for *Ceratosoma trilobata* (Gray) is "sponges", whereas *Hypselodoris capensis* (Barnard) is recorded only as preying upon a "light blue sponge". *H. capensis* may well be a specialist predator of only a single unidentified sponge species, but such data were considered inadequate for inclusion; similarly imprecise records for other nudibranchs preying upon multiple taxa were excluded from those particular species' dietary lists. Truly generalist predators, such as the species of *Bathydoris* (benthic carnivores) and *Melibe* (planktivores), also mostly were excluded because of lack of specific detail which would make comparisons problematic. However the rather more detailed information for *Melibe leonina* (Gould) and *Tethys fimbria* (L.) did permit their inclusion with a conservative number of prey taxa set at 10. Records of spurious diets for species observed in captivity also were removed, as were several instances of known synonymy of dietary species (e.g. *Anemonia viridis* (Forsk.) = *Anemonia sulcata* (Pennant)). Fish eggs (e.g. for *Calma glaucooides* (Alder & Hancock)), and nudibranch eggs (e.g. for *Favorinus branchialis* (Rathke)), were included here as a single dietary 'species' for those nudibranchs, irrespective of the species identity of the spawn. These alterations were, however, minimized in order to preclude personal subjectivity and overall the presented summary illustrations are almost identical to the sources reviewed by McDonald & Nybakken.

As outlined by McDONALD & NYBAKKEN (1997), numerous problems are presented here in terms of the reliability of the primary information. In many senses modern biologists are prisoners of the past, in that there is an obligation to rely upon the veracity of the reported dietary species and correct identifications. Difficulties also inevitably will arise from (historically generalist) species subsequently being split by taxonomists into a grouping of closely related but distinguishable specialists; but these problems are not insurmountable, so long as the original identifications were correct and reported in sufficient detail. The converse problem, of several apparently specialist species being subsumed into a single taxon is less acute. Intractable cases perhaps are best illustrated in the British Isles by *Doto coronata* (Gmelin), a common dendronotid predator of hydroids. *D. coronata* was for long recognised as being widespread and morphologically variable. In occurring both intertidally and sublittorally, and occupying a considerable geographic range, it is to be expected that numerous species would be recorded as its

diet. The data include almost certain incorrect attributions (e.g. the ctenostomatid bryozoan *Alcyonidium*), but the overwhelming majority of observations undoubtedly are correct. Only comparatively recently (LEMCHE, 1976; MORROW *et al.*, 1992) have specialist taxonomists commenced the task of differentiating morphologically distinct species within the complex "*Doto coronata*" that in the past certainly have been confused by numerous observers (ourselves included), and who are not taxonomists. It presently is impossible to confidently ascribe the true diet of *D. coronata* and even LEMCHE (1976) was uncertain as to whether or not *D. coronata* should remain a distinct species. Are, for example, all the records of *D. coronata* preying upon *Kirchenpaueria pinnata* (L.) attributable to the separation by LEMCHE (1976) of the specialist predator of that hydroid, *Doto dunnei* Lemche? The answer almost certainly is yes, but for the present the historical literature for the diet of *Doto coronata* places this species amongst the most generalist of nudibranchs world-wide.

Other than individual researchers making subjective judgements and deletions from prior records and thereby re-writing history, there is no reliable means of expunging even obviously fallacious observations from the literature. The possibility always will remain that *Acantbodoris pilosa* can consume a poriferan sponge, but *A. pilosa* is undoubtedly a specialist predator of ctenostomatid bryozoans. Similarly, the dietary records of cheilostomatid and ctenostomatid bryozoans, octocorallians and "dead fish" for the specialist barnacle predator, *Onchidoris bilamellata* (L.) undoubtedly are invalid. In adopting a conservative approach to the published data it is acknowledged that here only broad patterns which are robust and clear should be deduced. For the above reasons it also is apparent that the data do not warrant detailed statistical analysis, though some simple tests are included below to allow objective testing of general hypotheses and generalisations.

The frequency distribution of the number of dietary species for the 600 species of nudibranchs of known diet (Fig. 1) shows a clear overall pattern, despite the foregoing qualifications. Most obviously, 50% (298/600) of the species are recorded as preying upon a single species and 75% (454) as being associated with only 1-3 prey species. Given that the different suborders are primarily predators of rather different epifaunal taxa (e.g. Doridacea on especially sponges and bryozoans; Aeolidacea on cnidarians), it is notable also that the species of the four suborders show strikingly similar frequency distributions and degree of overall specialisation. Fisher's Exact Test shows no significant difference ($p = 0.352$) in the proportions of monophagous specialists among the four separate suborders. None the less, in terms of the generalisation regarding specificity of diet across the Order, it is important to note that half the species — for which there are data available — do apparently prey upon more than a single species.

But further care is necessary because the very nature of species listings is that the observations are qualitative and unweighted — that is, a single observation for one species cannot be quantitatively evaluated against multiple records of another species or against several different dietary species.

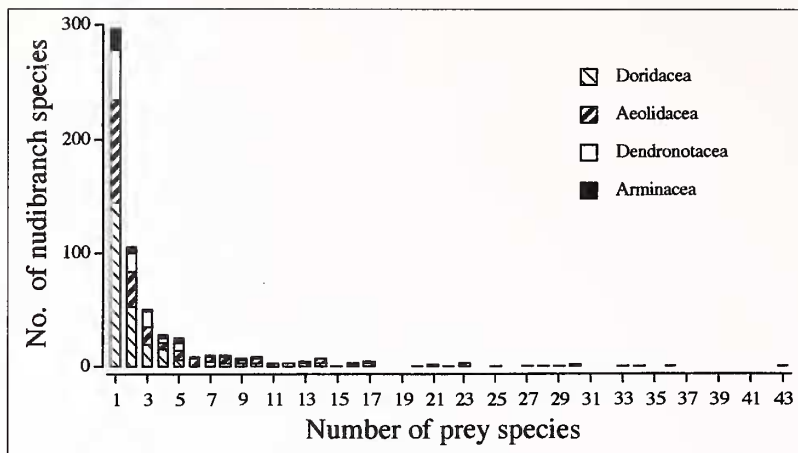


Fig. 1. Frequency distribution of numbers of dietary prey species for 600 nudibranch species (data from McDONALD & NYBAKKEN, 1997).

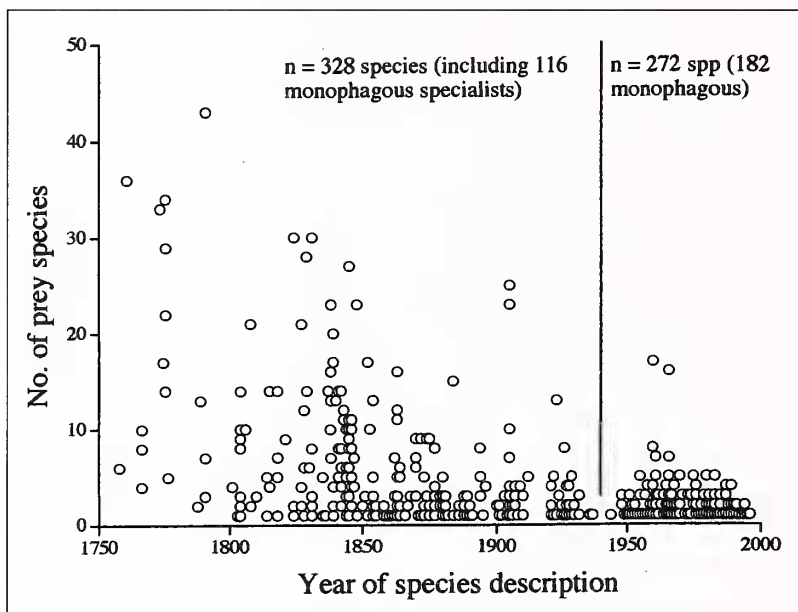


Fig. 2. Scatterplot of the numbers of reported prey species for each of 600 nudibranch species (data from McDONALD & NYBAKKEN, 1997) in relation to the year of their description. Monophagous specialists are recorded as preying upon one species only. The data were arbitrarily split into two groupings — those described pre-1937 and those post-1944 — for further analysis.

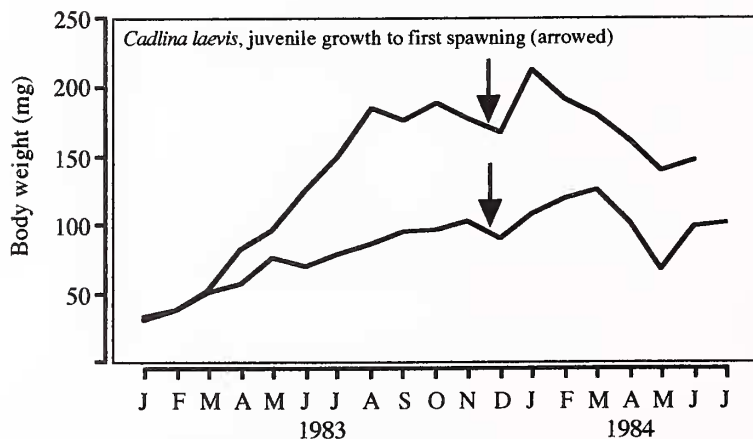


Fig. 3. *Cadlina laevis*. Growth of two example juveniles collected from the field in November 1982 and first weighed in January 1983; these would have hatched from the spawn mass ~April/May 1982. Both spawned for the first time in November 1983, at a benthic age of ~19 months.



According to the published records many specialist nudibranchs probably can exploit several prey species, but the likelihood is that many or most are clearly associated with, or prefer, just the one species (see, for example, MORROW *et al.*, 1992, on *Doto* spp.). In the British Isles *Adalaria proxima* is undoubtedly a specialist predator of the cheilostomatid bryozoan *Electra pilosa*; but it is not monophagous. From extensive field and laboratory observations we have recorded *A. proxima* occasionally feeding on *Callopora lineata* (L.) and very rarely on the ctenostomatids *Alcyonidium gelatinosum* (L.) (Syn. *A. polyoum* (Hassall)), *Alcyonidium hirsutum* (Fleming) and *Flustrellidra hispida* (Fabricius). Other examples of specialists which apparently are associated with (and cryptically camouflaged on) the one prey species in the British Isles include *Tritonia bombergi* Cuvier (on *Alcyonium digitatum* L.), *Tritonia nilsodbnieri* Marcus (on *Eunicella verrucosa* (Pallas)), *Cuthona nana* (Alder & Hancock) (on *Hydractinia echinata* (Fleming)), *Onchidoris inconspicua* (Alder & Hancock) and *Onchidoris sparsa* (Alder & Hancock) (on *Cellepora pumicosa* (Pallas)), and *Onchidoris depressa* (Alder & Hancock) (on *Schizomauvella linearis* (Hassall)): records do, however, exist of one or more additional dietary species for all of the latter nudibranchs (TODD, 1981).

Despite the frequency distributions for the four suborders being closely similar, there is one clear example of within-group heterogeneity which perhaps warrants closer scrutiny. The family Chromodorididae shows a significant difference (Fisher's Exact Test, $p = 0.018$) from other non-chromodorid Doridacea in the level of their apparent specialisation: 46 of the 70 reported chromodorids are monophagous, in contrast to only 100 out of 205 non-chromodorids. Do chromodorids differ fundamentally from other families within the Order? The Chromodorididae is essentially a tropical/sub-tropical family (RUDMAN, 1977) and these dorids typically are specialist predators of encrusting sponges. Notwithstanding the possibility that this family truly does show unusually subtle niche differentiation and a high level of dietary specialisation, other factors also might explain their seemingly anomalous status. Many of these species occur in biogeographic areas that are taxonomically relatively poorly-known and many chromodorids seemingly are relatively rarely recorded. Such cases inevitably will appear to be dietary specialists if the nudibranch species, or its diet, have been recorded for example only the once.

An alternative explanation might be that the dietary species are relatively poorly known for this family and thus the (few) attributable records convey the erroneous impression of stenophagy or even monophagy. Many chromodorids can be found actively preying upon sponges in the field, but commonly they are found either cryptically concealed or moving actively across the substratum and not associated with a particular prey organism. Dietary data from observation alone are therefore likely to be sparse. Scuba diving and submersible equipment have been available to biologists for only a relatively short period of time and direct and detailed *in situ* observations of sublittoral nudibranchs active in their natural habitat are therefore relatively limited and recent in a historical context. This constraint in the data has to be viewed in the knowledge that taxo-

nomic descriptions of nudibranchs date back to the application by Linnaeus of the binomial system to animals in 1758 (*Doris verrucosa* Linnaeus).

The historical context is important also in that additions to the listings of nudibranch dietary species (both correct and incorrect) are cumulative in the literature. It is to be expected that species described in the 18th and 19th centuries will by now generally have been reported as having more dietary species than will more recent discoveries and descriptions, unless the former are genuine monophagous specialists and published data are error-free. Fig. 2 shows the recorded number of dietary species in relation to the year of first description of the 600 nudibranch species. Whilst many monophagous specialists were first described during the 19th century, relatively fewer generalist species have been described more recently, although the dietary data for many recently described species probably are as yet incomplete. A comparison of the relative proportions of monophagous to non-monophagous nudibranchs described pre-1938 versus post-1943 (Fig. 2) shows a highly significant difference (Fisher's Exact Test, $p < 0.0001$). To an extent this probably reflects better current knowledge both of the predators and their actual and likely (or unlikely, e.g. "dead fish" or "dead anemone") prey items, as well as more rigour (e.g. MILLER, 1961) in the attribution of an organism as a dietary species for a given predator. The recent description of an apparently disproportionate number of specialists is not attributable to large numbers of new descriptions of (monophagous) chromodorids — only 17 of the 46 monophagous chromodorids were described post-1943. The most likely explanations are that (i) insufficient time has elapsed for the full dietary spectrum of some recently described species to be completed, (ii) there is improved scientific rigour in the identifications, observations and interpretations of nudibranch diets, and that (iii) genuinely specialist (monophagous) species are tending to predominate in the recent descriptions.

Monophagous predators can, by definition, display a distributional range only coincidental with that of their single prey species. But the possibility remains for functional monophagy of a stenophagous predator occupying a wide geographic range and exploiting different single species in given areas within that range; the outcome for that species would be for it to appear (in compilations such as the present) a relatively non-specific predator. Some chromodorids display a very wide geographic distribution (e.g. throughout the Indo-west Pacific); over such large distributional ranges it is perhaps inevitable that some apparently specialist, but widespread, predator species will have to exploit various prey species (e.g. the aeolid *Phestilla sibogae* on various species of *Porites*).

As knowledge improves of previously under-recorded areas — such as polar waters, the deep sea benthos, hydrothermal vents and coral reefs of oceanic islands — the world list of described species and their diets will inevitably increase. The more generalist predators will, in all probability, be the more widely distributed, perhaps the more common and thus the most easily found. Commonly found (generalist) species will tend to have the longer taxonomic history. In traditionally



long-researched and well described biogeographic areas, such as the coastal British Isles, recent descriptions are predominantly of monophagous or stenophagous specialists. The third of these possibilities therefore is of especial interest from the wider ecological perspective if it reflects covarying traits of rarity and specialism of diet amongst the Order as a whole. Because this Order includes such a wide variety of epifaunal predators, often preying upon numerically and structurally important epifaunal species within the community (e.g. long-lived anemones and octocorallians), they must offer ecologists considerable possibilities for empirical research on niche breadth, species abundance patterns and predator-prey dynamics (e.g. 'top-down' versus 'bottom-up' control in communities).

Despite the limitations of the data, the conjecture that the nudibranchs as a predatory group are characterised by species with marked dietary specialisations is tenable. Of course many of the seemingly generalist (polyphagous) species in Figs 1 and 2 prey upon multiple species within a single taxon (e.g. Porifera); therefore, at the higher taxonomic levels even these species undoubtedly remain specialised. But as with all ecological patterns there are clear exceptions; some species, such as *Hermisenda crassicornis* (AVILA *et al.*, 1998) and species of *Bathydoris* (WÄGELE, 1989) and *Melibe*, evidently are very much generalists in taking a heterogeneous array of benthic and planktonic prey items. Other species are irrefutably specialists in taking only a particular kind of prey and yet are relatively non-specific within that constraint (e.g. *Aeolidia papillosa* (L.) on anemones). Yet others eat one species only. Specialisation of diet thus remains a subjective judgment, but arguably is a feature that can be extended to the group as a whole.

LIFE CYCLE AND LIFE HISTORY VARIATION

Whereas useful data on the diet of nudibranch molluscs can effectively be compiled from short-term, incidental or anecdotal observations, similar information on longevity, life cycle and life history can be reliably attained only by extensive and repeated field and laboratory observation. Most nudibranchs are relatively small-bodied and quite probably are relatively short-lived. Many species, and most particularly those from higher latitude waters, typically are strongly seasonal in their occurrence and/or spawning activity. But in appraising the generalisation of their typically having annual/subannual life cycles, probably the greatest problem lies in assessing how representative of the Order are the species upon which published studies are available. Practically, long-term quantitative studies are constrained by the species being of suitable abundance or density and of consistent abundance over numerous seasons or years. Such studies for particular localities (e.g. EYSTER, 1980) or biotopes within localities (e.g. kelp epibionts; LAMBERT, 1991) are remarkably few in number and even then are typically restricted to a maximum of perhaps only 2 to 3 years duration. Given that species rarity is the ecological rule, the question has to be asked whether or not published studies have concerned the "sparrows", or the striking exceptions to the rule, within the Order Nudibranchia.

Strictly defined, semelparous organisms undergo a single

spawning event, as exemplified by some epitokous polychaete species in which the body wall ruptures on release of the gametes. Nudibranchs typically produce several spawn masses during a single reproductive season, perhaps of a few weeks or months duration, and copulate repeatedly between spawnings. Semelparity commonly covaries with such demographic traits as restricted longevity. Iteroparity, by contrast, concerns repeated and discrete spawning events or reproductive periods which are separated by a quiescent phase of gonadal regression, and this strategy commonly covaries with extended longevity. Nudibranchs can be considered semelparous (despite spawning repeatedly) in that having once attained maturity their period of spawning is inevitably followed by genetically programmed post-reproductive death. Spawning may be delayed by the absence of copulation but infertile spawns still are produced and the animal dies. Observations of the boreo-Arctic chromodorid *Cadlina laevis* (L.) have, however, shown that this species is very much an exception to other published studies.

Cadlina laevis may attain 30–40 mm in mantle length (up to ~260 mg live weight). This species is very unusual in undergoing true 'direct', nonpelagic embryonic development (THOMPSON, 1967): most cases of nonpelagic development in nudibranchs concern the shelled lecithotrophic veliger undergoing metamorphosis within the egg capsule (capsular metamorphosis) or soon after hatching. Embryos of *C. laevis* do not develop into a veliger as such and have only a transient and vestigial larval shell. Embryonic development results in a fully-formed benthic juvenile of 0.8–1 mm length hatching from the egg capsule. This species occurs both intertidally and sublittorally, is widespread in the North Atlantic and is most common in the British Isles on northeastern coasts. Spawning on the east coast of Scotland occurs in winter and, somewhat paradoxically, small intertidal juveniles (<10 mm) are found co-occurring in autumn with adults (~20–40 mm) that are approaching maturity, as indicated by the well-developed ovotestis clearly visible through the dorsum. Within the constraints of the above generalities on nudibranch life histories, two possible explanations appear most likely. First, this species might be annual in life cycle, but spawn aseasonally; alternatively, the life cycle actually might be biennial, with individuals reproducing only in their second year. Biennialism as a life cycle strategy is rare in both plants and animals, although several British nudibranch species are known to be biennial and semelparous, including *Archidoris pseudoargus* (Rapp), *Jorunna tomentosa* (Cuvier) and *Tritonia bombergi*. The latter three species all are notable in being relatively large and preying upon stable prey resources (e.g. *Archidoris pseudoargus* on the sponge *Halicbondria panicea* (Pallas)) which are predictably available year-round.

Cadlina laevis is a predator of slime sponges and laboratory observations indicate this to be a specialist on *Halisarca dujardini* Johnston which also persists year-round; individuals can be maintained throughout the life cycle on *H. dujardini* alone, but in the field it is seldom associated with any prey organism. The laboratory maintenance of 10 juvenile individuals (4–5 mm at collection in autumn) reared under ambient temperature (3.5–20°C) and photoperiod in through-flow aquaria over 3.5 years,



revealed the growth of this species to be extremely slow (Fig. 3). Respirometric data showed low metabolic rates which, in contrast to the strictly annual *Adalaria proxima* and the biennial *Archidoris pseudoargus* (Rapp), were relatively insensitive to temperature (Fig. 4). Composite data for 28 *C. laevis* also collected in the autumn, but as larger individuals, ongrown in the laboratory for 3.5 years (Fig. 5) not only confirmed the slow growth and extended life cycle, but demonstrated that reproduction first occurs when individuals are ~1.5-2 years old. Annual reproductive effort (turnover ratio; HAVENHAND & TODD, 1988b/1989) and fecundity both are low (32%; 10^2 - 10^3 eggs, respectively) and packaged as a single spawn mass in any one year. Adults survive after spawning and may well spawn once per year another two or three times and attain an age of 5-6 years. Furthermore, many individuals showed a very atypical pattern of post-spawning somatic growth, compared to annual species (e.g. *Aeolidia papillosa* (HALL & TODD, 1986), *Adalaria proxima* and *Onchidoris muricata* (HAVENHAND & TODD, 1988a, 1989)), in attaining a midsummer peak in size followed by a decline towards spawning in the subsequent winter. The body sizes of individuals in their later spawning seasons often were smaller than the maximum achieved during the second year of life (e.g. Fig. 5). Thus, other than allowing the distinguishing of young 0+ juveniles, body size is a totally unreliable indicator of age in this species which is atypical in displaying both a perennial life cycle and iteroparity.

Given that generally little is known of the reproductive strategy of most species of nudibranch, other than perhaps egg sizes and larval type (e.g. HADFIELD & SWITZER-DUNLAP, 1984; HADFIELD & MILLER, 1987), these data for *Cadlina laevis* suggest that caution should be extended in presuming that nudibranch species conform to the preconception or generalisation of invariable annual/sub-annual life cycles and semelparity. Extended life cycles and iteroparity may be far more widespread traits among those species which are insufficiently common for quantitative population analysis in the field, or for which laboratory rearing has not been attempted or proven possible. Although adult size alone is not a reliable indicator of either life cycle or life history, the likelihood is that especially other large-bodied nudibranch predators of sponges in the British Isles (e.g. *Geitodoris planata* (Alder & Hancock)) and elsewhere also are longer-lived biennials or perennials, and that iteroparity may yet be comparatively widespread in both tropical and temperate waters.

EGG SIZE VARIATION AND LARVAL TYPE

HADFIELD & MILLER (1987) reviewed the egg sizes of opisthobranch molluscs. Amongst the difficulties they encountered were different authors reporting different egg sizes for the same species and instances of the same author(s) reporting different egg sizes for the one species in different studies. Despite this, their compilations have proven very valuable in allowing interpretations of broad patterns of distributions of egg sizes in relation to the different larval developmental types within both the Nudibranchia (250 spp) and the Opisthobranchia in general (369 spp). Reproductively active nudibranchs often spawn

within a few hours of retrieval to the laboratory irrespective of whether or not they are maintained on their dietary species; this behaviour is convenient for the compilation of egg diameter measurements and permits the likely assumption that the reported species provide an unbiased sample of the Order. HADFIELD & MILLER (1987) showed that most nudibranch species have planktotrophic larvae which hatch from relatively small eggs (zygote diameter range ~50-170µm; mode ~75µm). Nonpelagic lecithotrophic species display the largest eggs (range ~100-380µm; mode ~205µm), with pelagic lecithotrophic species generally intermediate (range ~100-220µm; mode ~135µm).

Despite the uncertainties of the precision of the data (HADFIELD & MILLER, 1987), these patterns are both clear and conform to expectations of relationships between egg size and larval type in other groups of marine invertebrates (JABLONSKI & LUTZ, 1983; GRAHAME & BRANCH, 1985; HAVENHAND, 1995; WRAY, 1995; MCEWARD & JANIES, 1997; PECHENIK, 1999). But given that HADFIELD & MILLER (1987) utilised only mean values it is of interest also that there is considerable overlap of the data, in that the largest reported planktotrophic egg size (~165µm) also is firmly within the range more typically associated both with pelagic and nonpelagic lecithotrophic development. If nothing else, this is persuasive in showing that planktotrophic nudibranchs are not subject to selective pressures to minimize egg size (and hence maximize egg numbers) (see also MCEWARD, 1997). Setting aside the possibilities of additional embryonic resource provisioning by extrazygotic yolk (a feature widespread amongst ascoglossans; BOUCHET, 1989), if one allows that (i) lecithotrophy demands more reserves per embryo and (ii) that there is a general evolutionary progression from (primitive, ancestral) planktotrophy towards (advanced, derived) lecithotrophy (e.g. STRATHMANN, 1985), it follows (iii) that egg size increases are an essential requirement in the evolution of lecithotrophy (KEMPF & TODD, 1989). The implications are, however, that there is a minimum egg size (~55µm) below which the nudibranch larval form cannot be supported.

From Hadfield & Miller's data it is obvious that egg size alone is not the sole determinant of larval strategy, although lecithotrophy is seemingly not supportable by egg sizes characteristic of most planktotrophic species (50-100µm). Lecithotrophic development differs fundamentally from planktotrophy in many ways other than the embryo simply developing from a larger egg. Larval swimming and food capturing organs differ between the two, as do structures of the gut and the capacity for larval feeding; note also that despite being carnivorous as adults, these planktotrophic larvae are essentially consumers of particulate plant material and this will require biochemical and morphological changes in gut structure through metamorphosis (BICKELL *et al.* 1981; KEMPF & TODD, 1989; TODD, 1991). The levels of ontogenetic development at hatching also differ markedly, especially in the development of foot musculature and the larval sensory systems. At hatching, planktotrophic larvae of nudibranchs have no propodium and generally lack eyes, though there are some exceptions to the latter (HIRANO & HIRANO, 1991), whereas all lecithotrophic larvae



have a well-developed foot and eyes at hatching. Thus, although a component pre-requisite for support of lecithotrophic development, a larger egg does not simply confer transition from planktotrophy to lecithotrophy.

INTRA-SPECIFIC VARIATION IN EGG SIZE: ARE ALL EGGS EQUAL?

Although compilations such as those of HADFIELD & MILLER (1987) are valuable in revealing general trends and patterns in the development of opisthobranchs, allowance cannot be made for intraspecific variation in egg size. There is no reason to suppose that egg size as a trait should be fixed for any one species. Here we ask the questions; to what extent does egg size vary within species, and does such variation have adaptive potential? The focus of our studies has been *Adalaria proxima*, a common dorida which is widely distributed throughout the northern

British Isles. Its range includes NE England, all of Scotland, N Wales and N Ireland. It is strictly annual in life cycle and reproduces by means of pelagic larvae. Metamorphosis is induced by a water-soluble moiety derived from the prey bryozoan, *Electra pilosa* (LAMBERT *et al.*, 1997), but never occurs within the capsule. The larvae can feed (KEMPF & TODD, 1989) but do not have to feed to complete metamorphosis and they thus are categorised as pelagic lecithotrophic. Post-spawning mortality of adults is absolute and recruitment of the subsequent generation is from pelagic larvae.

Although the dispersal potential of this species is not as high as sympatric planktotrophic counterparts (e.g. *Goniodoris nodosa* (Montagu), TODD *et al.*, 1998), laboratory observations suggest that a pelagic life of several days is not unusual, and delay of metamorphosis may extend to >2 weeks. Adult *Adalaria proxima* were sampled for the 1993-94 generation from five inter-

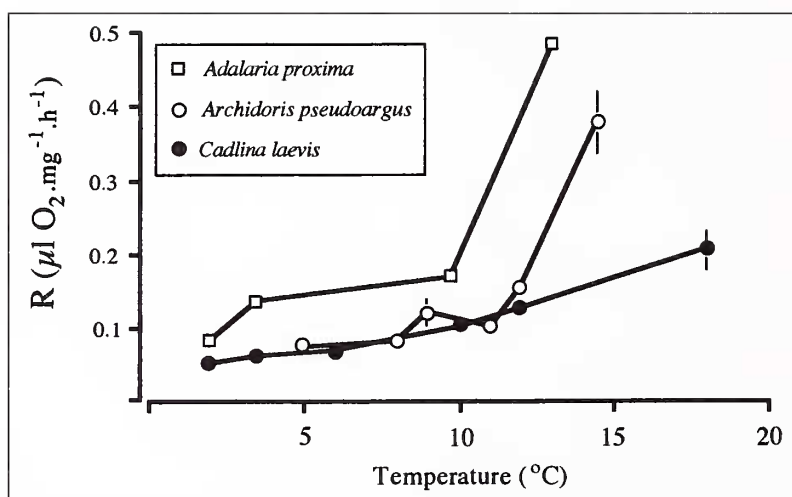


Fig. 4. Respiration rates (R , weight specific consumption of oxygen), over the seasonal temperature range, for the annual semelparous dorida *Adalaria proxima* (data from HAVENHAND & TODD, 1988a), the biennial semelparous *Archidoris pseudoargus*, and the perennial iteroparous *Cadlina laevis*. *Cadlina laevis* shows relative insensitivity to temperature. Error bars for *A. pseudoargus* and *C. laevis* are \pm s.e.

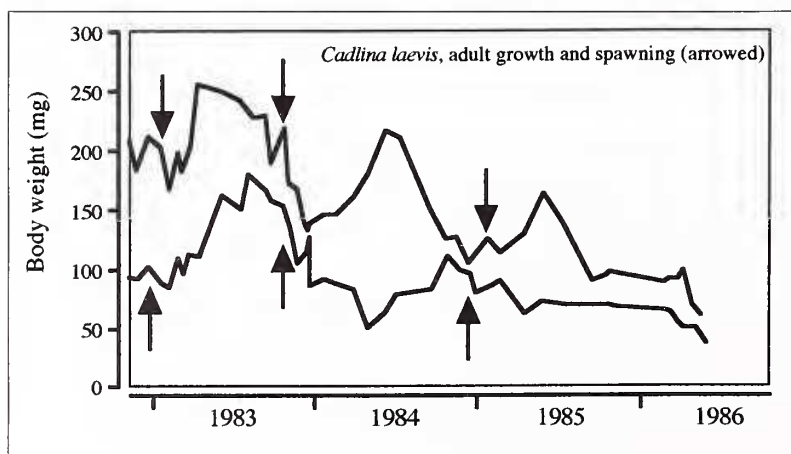


Fig. 5. *Cadlina laevis*. Growth and spawning of two example adults first collected in October 1982. Each spawned once only in each of three successive winters over ~ 3.5 years in the laboratory and probably were 5 or 6 years old at death. Note that annual spawning did not coincide with peak weight in that year and that there was progressive degrowth with age.



tidal locations embracing that geographic distribution. A total of 184 adults were collected just prior to spawning and Fig. 6 shows the mean egg (zygote) diameter measured for 159 spawn masses laid in the laboratory: only those spawns which had yet to commence cleavage could provide the required egg size data. The observed mean range of 149–192 μm is considerable, resulting in the larger eggs having 214% the volume of the smaller. Particularly striking is the between-population variation and the consistent pattern of within-population variation in egg size. Assuming that water content and biochemical provisioning of those eggs are proportionally similar, it is evident that all eggs are not equal and that in the extreme some embryos have more than double the reserves of others.

The implications for this on size and 'quality' of embryos are obvious and these differences may well be reflected in similar variation in larval size and 'quality' in terms of metamorphic success, size at metamorphosis and post-settlement growth potential of the juvenile. Such differences in egg size may therefore exert cascading adaptive influences on fitness of individuals. Alternatively, this between-population variation may simply reflect differing environmental conditions (e.g. local habitat variation in abundance of prey bryozoans), because those adults were collected from the different field locations having almost completed their pre-reproductive growth. In August 1992 post-metamorphic juveniles (1–2 mm mantle length) had been sampled for the 1992–93 generation from five sites, including Portaferry and Menai Bridge. The 1992–93 juvenile populations all were reared for 9+ months to spawning (Fig. 7) in the laboratory under identical (field ambient) temperature and photoperiod conditions. Mean egg sizes for the two illustrated Menai Bridge populations showed no significant difference between years (180 μm , $n = 49$ spawns, 1992–93; 181 μm , $n = 21$ spawns, 1993–94; $t = 1.206$, $P = 0.232$), but there was a significant difference for Portaferry (162 μm , $n = 87$, 1992–93; 157 μm , $n = 21$, 1993–94; $t = -6.353$, $P < 0.001$) (Figs 6, 7). Given the small sample sizes for 1993–94 some discrepancy might be expected but, notwithstanding the between-year difference for Portaferry, there is a clear consistency of the between-habitat contrasts for these (and other) sample sites. Because the 1992–93 populations were reared from early post-metamorphic juveniles, under identical conditions and fed to excess, we are confident that these between site differences in egg sizes are largely genetically determined (LAMBERT *et al.*, 2000).

The data in Figs. 6 and 7 are for groups of individuals from the respective populations. Previous analyses (JONES *et al.*, 1996) have shown that individuals' first-laid spawn masses generally are the biggest clutches and also include their largest eggs. Later spawnings typically are of smaller clutches of smaller diameter eggs. Again, assuming that egg volume is a direct measure of embryonic provisioning by the adult, later-produced eggs are likely to be of lower 'quality' than those spawned earliest. Estimates of fecundity, as indirect measures of individual fitness, such as those that we have undertaken in the past (e.g. TODD, 1979; HALL & TODD, 1986; HAVENHAND & TODD, 1988b) probably are therefore quite inappropriate if these egg

size differences do indeed reflect differing quality of offspring.

All eggs are not equal, and this reflects ecological variance which is of considerable potential importance. But is this variation adaptive? Do larger eggs give rise to larger, higher quality larvae which have better survival through metamorphosis, and do those larger metamorphs give rise to larger, fitter reproductive adults? Laboratory culture of sampled populations maintained throughout their benthic life to spawning (LAMBERT *et al.*, 2000) showed no simple between-population pattern of reproductive strategy. Each of the five populations investigated appeared to display a unique combination of the following traits; individual growth rate, typical size of spawning adults, egg size, number and size of spawn masses, duration of spawning period, overall reproductive effort and capsular development time for larvae (JONES *et al.*, 1996). These patterns were consistent within populations and it remains uncertain as to whether these differences are attributable to local habitat selection or to neutral effects attributable to random genetic drift of essentially isolated populations. Presently, however we lean to the latter explanation (LAMBERT *et al.*, *op. cit.*) because of the clear and temporally predictable patterns of genetic differentiation of *Adalaria proxima* around the British Isles (TODD *et al.*, 1998); these are indicative of essentially local larval colonisation of pelagic larvae within demographically closed populations.

Restriction of between-population gene flow for *Adalaria proxima* is indicated by the very high degree of differentiation between discrete field populations separated by distances of only a few hundreds or thousands of metres in localities subject to intense tidal currents of up to $\geq 3 \text{ m s}^{-1}$ (TODD *et al.*, 1998). Measures of between-population genetic differentiation for *A. proxima* are of the level more typical of nonpelagic lecithotrophs (TODD *et al.*, *op. cit.*). Larval dispersal therefore appears to be minimal in *A. proxima*, despite laboratory observations of larval longevity indicating that the pelagic lecithotrophic veliger has the potential to disperse considerable distances and to confer at least moderate levels of gene flow between populations. This is presumed to result from behavioural adaptations preventing larvae from entering the water column: those that do become entrained in the water column essentially are lost but longer distance colonisation of new habitats must still very occasionally occur.

Variability in individual larval behaviour may be crucial in this context, in that developmental variability within or between clutches may confer variation in swimming behaviour and thence dispersal/colonization potential. Such variability may be driven by differences in egg size (Fig. 6), and hence the resources provisioned to larvae, and vary both between and within populations and individuals over their spawning lifetime. Certainly, that the larvae of *A. proxima* can feed, but do not have to feed to complete metamorphosis (KEMPF & TODD, 1989), indicates a degree of plasticity not afforded to strictly nonfeeding lecithotrophs (see also MILLER, 1993 for *Phestilla sibogae*). Further investigation of the possible adaptive significance of egg size variation on survivorship, growth and fitness is evidently expedient.



EGG SIZE VARIATION AND EVOLUTION OF LARVAL TYPES

By definition, nonpelagic lecithotrophy demands greater parental investment in individual eggs than does planktotrophy; therefore egg size tends to covary with larval type. None the less, as HADFIELD & MILLER (1987) showed, the fundamental categories of planktotrophy, pelagic lecithotrophy and nonpelagic lecithotrophy each embrace a range of overlapping egg sizes and there are representatives of each category showing egg sizes within the range 100–170 μm . Given that egg size is never fixed for a species or individual, it is inevitable, therefore, that variation within the group as a whole can essentially only be directional — that is for egg size to increase over ecological time. Perhaps this simple statistical feature provides the impetus for selection for increased egg size which must accompany, but not be the sole determinant of, the acquisition of lecithotrophy (KEMPF & TODD, 1989). However, since the individual reproductive adult's resources are finite there will likely be some form of balancing selection to reduce egg size (and maximize numbers), resulting in a continuum of egg sizes and larval types (MCEDWARD, 1997).

As the above observations on larval dispersal in *Adalaria proxima* have shown, the state shift from (presumed ancestral) planktotrophy to (derived) pelagic lecithotrophy may well be facilitated by the genetic consequences of lecithotrophy resulting in genetically isolated (demographically closed) populations; such an evolutionary progression is not, therefore, simply attributable to egg size variation alone. That egg size differs so markedly between populations (Figs. 6, 7) indicates how this can become fixed for populations. But the question remains as

to whether or not this variation is adaptive: the indications are that these levels of intraspecific variation in egg size, although striking, are not adaptive and merely reflect drift of differentiated populations (JONES *et al.*, 1996; LAMBERT *et al.*, 2000).

VARIATION IN INDIVIDUAL REPRODUCTIVE BEHAVIOUR

Dioecy does not occur amongst nudibranch species and generally the Order has been categorised as displaying simultaneous hermaphroditism (TODD, 1981; HADFIELD & SWITZER-DUNLAP, 1984). In a wider ecological context there is much current interest in sperm competition and sex allocation in hermaphroditic species (e.g. GREEF & MICHIELS, 1999). In the past, a widely-held perception has been that the differential requirements in provisioning individual sperm and oocytes imply that sperm (and the male sex) could be considered 'cheap'. However features of especial current interest include the conjecture that an increase in sperm competition should occur with increases in multiple mating of individuals — 'first male precedence' *versus* 'last male dominance'. Another is that an elevation in investment in the male sex should result from either or both of sperm digestion and the obligatory reciprocal transfer of sperm. All of these features can lead to an equal investment in the two sexes by internally fertilizing hermaphrodites. Given the ease of rearing and maintaining many nudibranch species in the laboratory, the group would appear to be well-suited model systems for such investigation. Many aspects of reproductive behaviour of nudibranchs are poorly understood, but it is highly likely that reciprocal transfer of sperm is obligatory during copulation and the widespread occurrence of multiple or profligate mating of

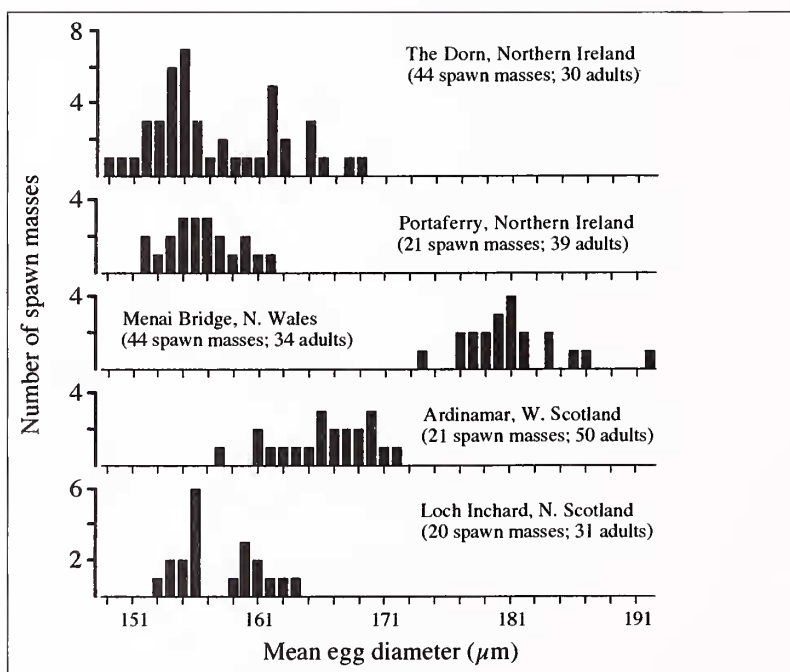


Fig. 6. *Adalaria proxima*. Mean egg diameters (microns) for spawn masses laid by groups of individuals (1993–94 generation) collected from five field sites as pre-spawning adults (February 1994). The site location details are given by TODD *et al.* (1997a).



individuals between spawnings, and the presence of a gametolytic (sperm digestion) gland, lead to the expectation that sperm competition may be of considerable ecological importance in this group.

Phostilla sibogae illustrates the potential for investigating variation in individual reproductive behaviour amongst this group (TODD *et al.*, 1997). We showed that sperm storage and multiple 'paternity' of an individual's zygotes is common in this species. More important, far from being a simultaneous hermaphrodite, *P. sibogae* is functionally male at an extremely small body size and sperm exchanged (and stored) as a juvenile are disproportionately successful in fertilizing oocytes in fully grown adults (TODD *et al.*, *op. cit.*). As spawning adults, however, individuals do function as simultaneous hermaphrodites. Early juvenile insemination possibly does not occur for all individuals in the field, but it is prevalent in laboratory cultures. Even if at relatively low frequencies in the field, such behaviour is likely to be strongly selected for in this species because of the intensity of fish predation (e.g. GOCHFELD & AEBY, 1997) and the likelihood of the few individuals which survive to an adult size failing to locate an adult mate: large spawning adults are seldom found in the field and copulation between individuals differing markedly in size is presumably unlikely.

For this species at least, therefore, there appears to be a strong selective advantage in fertilizing and being fertilized early — that is, first male/partner precedence. The earliest received sperm are very few in number but disproportionately successful, perhaps as a result of receiving nutritive gain or capacitation advantage over later-received sperm, or even to being less vulnerable to digestion by the gametolytic gland. Whether similar reproductive variability is widespread amongst the Order remains to be ascertained because assessments of genetic non-conformity of offspring and parents have been made for only this one species; but the fact that most nudibranch species typically are rare, or at least of low population densities, and that all are obligate cross-fertilizers are strongly indicative that it ought to be.

SIZE ASSORTATIVE MATING

Size assortative mating is a "positive correlation between the sizes of mates within a population or sample" (ARNQVIST *et al.*, 1996), and assortative mating "sexual reproduction involving the non-random pairing of individuals which are more closely alike than the average (positive) or less alike than the average (negative) in respect of one or more traits" (LINCOLN *et al.*, 1982). In dioecious species showing a positive relation between size and fecundity of females, there is an apparent selective advantage for males to copulate with larger females. However, the time invested in copulating with an individual female, and the amount of sperm that should be transferred renders the situation complex. This is especially pertinent for nudibranchs, amongst which multiple copulation is prevalent and given the foregoing problems associated with sperm dilution. For hermaphrodite species this becomes even more intricate, especially if reciprocal transfer of sperm is obligatory, because individuals can maximize their fitness both as a male and female. For

smaller individuals, the advantage in fertilizing (and being fertilized by) a larger individual is clear but the reverse is not. Even for strongly seasonal species, in which all individuals are of closely similar age, marked variation in size at reproduction is apparent. Fig. 8 shows the length frequency distribution for an intertidal population of the barnacle predator *Oncbidoris bilamellata*. As expected, the distribution is unimodal but the length range is considerable and body mass of this species increases by a factor of 5 for a doubling of length. The effective breeding population in Fig. 8 will be fewer than the 206 individuals sampled because the smallest dorids probably will fail to produce spawn. The effective population size probably will be yet smaller, because of limited numbers of suitably-sized mates for large and small individuals, unless there is strong positive assortative mating for both smaller and larger individuals.

The potential for nudibranchs as model systems in assessing assortative mating both in the laboratory and field is apparent from such size distribution data alone, but morphological problems probably also are implicated in pair formation in nudibranchs. Opisthobranch reproductive systems are structurally complex, and the manner in which the penes of copulating individuals become interlocked indicates major mechanical difficulties for copulation between individuals of markedly differing size. This variable becomes especially acute when considering how much these animals degrow during their reproductive period (e.g. HAVENHAND & TODD, 1988b). But is it just the body wall that shrinks (= 'deflates'), or do all the body organs degrow allometrically? If nudibranchs are limited in the size range of partners with which they can copulate, does that size range (and hence the number of potential partners) change during the individual's reproductive period? In the absence of assortative mating, do individuals of intermediate size have the greatest range of potential partners available, and do they therefore elevate their fitness over larger counterparts by maximizing their male function? These and related questions have yet to be assessed for nudibranchs.

POECIOLOGY

Developmental variability amongst marine invertebrates is perhaps expressed at its most extreme by the condition of poecilogony, and studies of opisthobranchs have provided some controversial examples (HOAGLAND & ROBERTSON, 1988; BOUCHET, 1988; CHIA *et al.*, 1996). Poecilogony can be defined as "intraspecific variation in the duration of ontogenetic stages induced by environmental factors" (LINCOLN *et al.*, 1982), but larval ecologists have utilised the term specifically to categorise those species which produce offspring which are separable according to their larval type. The latter application conforms to the previous definition in being quantitative (the egg-to-juvenile period differing in duration according to larval strategy; see also HAVENHAND, 1993) but it also is qualitative because of the contrasting morphology and ontogeny of the offspring. Poecilogony is seemingly very rare amongst marine invertebrates and essentially confined to polychaetes and opisthobranchs (BOUCHET, 1989; GIBSON, 1995; GIBSON & CHIA, 1995; CHIA *et al.*, 1996), and there are sound theoretical



grounds for supposing that selection should favour one strategy or the other, but not either/or within a species. Many suspected cases of poecilogony — especially those concerning geographically disjunct populations displaying contrasting larval types — have proven to involve cryptic species (HOAGLAND & ROBERTSON, 1988; HIRANO & HIRANO, 1991; CHIA *et al.*, 1996), but it is of interest that amongst opisthobranchs, and ascoglossans and nudibranchs in particular (BOUCHET, 1989), there now are several cases of poecilogony — albeit that these examples are open to differing interpretations (e.g. CARROLL & KEMPE, 1990).

For the small hydroid-grazing aeolid, *Tenellia adspersa* (= *pallida*) (Nordmann), EYSTER (1979) deduced poecilogony (pelagic larvae and capsular metamorphosis) in disjunct and single populations respectively, but the possibility of two sympatric cryptic species cannot be eliminated because single

egg masses and individual adults gave rise to only the one larval type. EYSTER (1979) did not culture the pelagic veligers of *T. adspersa* through metamorphosis, but her illustration of the hatched larvae (her Fig. 2A) is indicative of a planktotrophic larva, in that the somatic tissues within the shell and the foot development are minimal and there are apparently no eyes. If truly a case of poecilogony, this therefore would be an example of planktotrophy/lecithotrophy. For apparently the same species, CHESTER (1996) subsequently showed clear developmental plasticity in response to food availability to the individual reproductive adult, but this did not involve planktotrophic larvae; starvation of *T. adspersa* resulted in fewer, smaller eggs, all of which hatched as pelagic lecithotrophic veligers whereas control animals fed *ad libitum* showed 10–15% of offspring undergoing capsular metamorphosis.

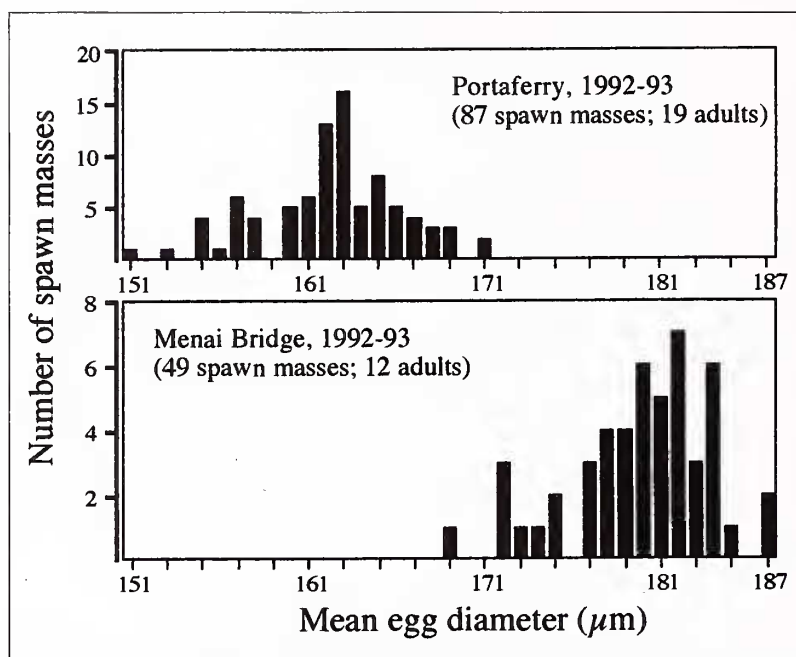


Fig. 7. *Adalaria proxima*. Mean egg diameters (microns) for spawn masses laid by 19 individuals (1992-93 generation) collected from the two field sites as post-metamorphic juveniles (1-2 mm) in August 1992. Individuals were reared to spawning for 9+ months under identical temperature/photoperiod and feeding conditions. See Fig. 6 and text for details of the between-year comparisons of mean egg sizes for each site.

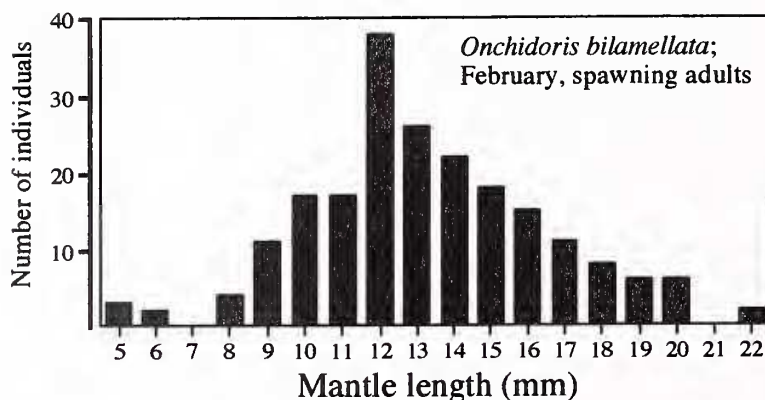


Fig. 8. *Onchidoris bilamellata*. Length frequency histogram for 206 individuals sampled intertidally (Robin Hood's Bay, NE England) at peak spawning (February 1975).



CHESTER (1996) found that capsular metamorphosis not only declined to zero on starvation of adults, but that it could be regained to levels of 32% of larvae produced by adults given access to food again. The need for molecular genetic studies of this species is clear in order to resolve the taxonomic issues: one or more species may or may not be involved, but true poecilogony is apparent.

CARROLL & KEMPF (1990) observed hatching of pelagic lecithotrophic larvae or of (capsular metamorphic) fully-formed benthic juveniles of the anemone predator, *Berghia verrucicornis* Costa, according to whether or not spawn cultures were aerated in culture. Whether this is true poecilogony is open to argument, and of particular relevance here is whether or not encapsulated larvae can acquire and respond to a prey-derived metamorphic cue or if capsular metamorphosis is not cue induced. Although the presence of the prey anemone, *Aiptasia pallida* (Verrill), resulted in significantly higher metamorphosis of larvae, CARROLL & KEMPF (1990) noted that a specific habitat-related cue was not obligatory for metamorphosis to occur. The possibility remains that *B. verrucicornis* merely displays a behavioural variation that leads to non-specifically induced metamorphosis occurring a little earlier or later. Although not a case of poecilogony in the strict sense, this species may present an evolutionary transitional state between pelagic and nonpelagic lecithotrophy as discussed elsewhere (KEMPF & TODD, 1989).

Amongst the opisthobranchs, without doubt the most extreme, and best documented, case of poecilogony is the ascoglossan *Alderia modesta* (Lovén), a specialist grazer of the alga *Vaucheria longicaulis* Hopppaugh. Larvae of *A. modesta* metamorphose in response to waterborne and surface-associated carbohydrates and KRUG (1998) has demonstrated both planktotrophy and pelagic lecithotrophy in the one species, as confirmed by mtDNA sequencing. Most spawn masses developed either as planktotrophic or pelagic lecithotrophic larvae, but a very few (1%) showed the full range of egg sizes and a mixture of planktotrophic and lecithotrophic veligers. This is rather different to the apparent case of poecilogony in the tropical ascoglossan *Elysia cauze* Marcus (CLARK *et al.*, 1979), in which the spawn masses from a single mollusc were of the one developmental type but the incidence of Types 1 (planktotrophic; spring), 2 (pelagic lecithotrophic; summer) and 3 (nonpelagic lecithotrophic; autumn/winter) development varied seasonally. As reviewed by HOAGLAND & ROBERTSON (1988), there are some taxonomic uncertainties in this example; the possibility remains that more than one species was involved and all spawn masses and adults displayed only the one developmental type.

Switching of development of nudibranchs between pelagic lecithotrophy and capsular metamorphosis is conceptually easy to envisage if it were attributable to, say, pleiotropic effects of perhaps only a few genes leading to small temporal shifts in competence and metamorphosis in the absence of a specific inductive cue (e.g. *Berghia verrucicornis*, CARROLL & KEMPF, 1990). A more problematic case, however, is the cephalaspidan *Haminaea callidegenita* Gibson & Chia (GIBSON, 1995;

GIBSON & CHIA, 1995), which also has lecithotrophic development, and which may undergo either capsular metamorphosis or release of lecithotrophic larvae, the latter with a potential pelagic life of up to 30 d. The incidence of capsular metamorphosis in *H. callidegenita* shows extreme variation among spawn masses, populations and years; functionally, therefore, poecilogony in this species is much more complex than for *B. verrucicornis* in view of the potential longevity of the pelagic larval stage. Although the percentage of hatching form (benthic juvenile or veliger) of *H. callidegenita* varied 4-100% between years, populations and clutches, all individuals showed variability in this trait. The developmental shift was not attributable either to adult or embryonic culture conditions, but adult food stress did appear important. Food deprived *H. callidegenita* initially produced more swimming larvae than did control females (GIBSON & CHIA, 1995).

Notwithstanding the foregoing, the genetic, cellular and ontogenetic basis of extreme poecilogony, involving the switch between planktotrophy and lecithotrophy, is much harder to envisage because that evolutionary shift demands changes not simply in egg size/embryonic resources (cf. WRAY, 1995). Alterations at the tissue, cell and subcellular levels — especially in relation to food capture/locomotion, feeding, digestion and overall development of the sensory and motor nervous systems (KEMPF & TODD, 1989) — are necessary in the shift from planktotrophy to lecithotrophy. The deployment of extrazygotic yolk within the stroma of the spawn mass is not infrequent amongst ascoglossans and may be a major factor explaining developmental variation across the Opisthobranchia (BOUCHET, 1989). None the less, *A. modesta* undergoing extreme poecilogony in the absence of extrazygotic yolk indicates the possibilities of more examples occurring within the Nudibranchia.

If extreme poecilogony proves to be a more widespread (if not common) strategy than is presently known, such variation presents evolutionary ecologists with a challenging puzzle, and all the more so if it is a feature characteristic of just polychaetes and opisthobranchs (CHIA *et al.*, 1996). Furthermore, as discussed by CHIA *et al.* (1996), reduced salinity appears to be a related factor in many examples. CHESTER (1996) reared *Tenellia adspersa* at a reduced salinity of 20 ppt but did not address the possible influence of salinity variation on developmental type. Notwithstanding such gross environmental effects, the levels of interspecific and intraspecific variation in such fundamental traits as egg size (e.g. Figs 6, 7) and the range of larval types displayed by nudibranchs leads to the tantalizing suggestion of there being a high probability of many more novelties yet to be discovered. But the question remains as to whether or not such variation is truly adaptive.

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